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PAPERS.

16. On the Structure of the Skull in *Chrysochloris*.

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(Plates I., II.* and Text-figures 1–3.)

The examination of the Organ of Jacobson and the nasal cartilages in the Cape Golden Mole, the results of which I recently communicated to the Society †, showed that *Chrysochloris* is not, as has been generally held, an ally of *Centetes*, nor indeed apparently of any of the small mammals which are usually grouped together as "Insectivora," and that the Golden Moles ought to be placed in an Order by themselves to which Dobson's name of Chrysochloridea may be applied. As the type is so unique, it seemed worth while to make a careful study of the skull.

Hitherto very little has been known of the skull of *Chrysochloris*. Though the animal is not at all rare, it is not often seen unless specially looked for, and probably only a very small proportion of the inhabitants of South Africa have ever seen one, except perhaps in a Museum. Most of the larger museums have a number of skins and skulls, but, as is the case with many small mammals, the cranial bones in the adult are so completely

* For explanation of the Plates see p. 458.
† P.Z.S. 1915, p. 347.

anchylosed that it is impossible to do much more than speculate on the structure. Dobson figures a nearly adult skull of one species which reveals some sutures, but only a very young skull could clear up most of the points in doubt, and until recently, so far as I am aware, no very young specimens have ever been obtained by any scientist. While residing at Stellenbosch, though I collected many adult *Chrysochloris*, I only succeeded in getting about half a dozen young specimens, and unfortunately I have no specimens which would show the early condition of the chondrocranium. Still, the skull of the newly-born *Chrysochloris hottentota*, which I have examined, is in such an interesting stage of development that it reveals clearly the nature of practically all the cartilaginous as well as the osseous elements.

Prof. J. P. Hill has very kindly had the head of the young *Chrysochloris hottentota* sectioned for me by his laboratory assistant, Mr. F. Pittock, and the facts revealed in the sections have been confirmed and amplified by the study of a prepared skull of a slightly older *Chrysochloris asiatica*.

Skull of young Chrysochloris asiatica.

The skull measures in greatest length 13·5 mm., and the basal length from the basioccipital to the premaxilla is 10·7 mm. The maximum width is 9·5 mm., and height 7·5 mm.

When viewed from above, the large size of the brain region, the narrowed orbital, and the short narrowed facial region give the skull a slight superficial resemblance to that of a small bird.

The premaxillæ are small, irregularly square-shaped bones which articulate by one side with the maxillæ and by another with the nasals. They contain the already calcified points of the three milk-incisors. The premaxilla forms a distinct portion of the hard palate behind the incisors and in front of the anterior palatine foramina.

The maxilla forms the greater part of the hard palate. Already the milk-canine, the three milk-molars, and the first molar are partly calcified. The maxilla forms about twice as large a part of the side of the snout as does the premaxilla. There is a large foramen for the large maxillary branch of the Vth nerve. The most remarkable thing about the maxilla is the way in which it forms the jugal arch. There is no trace of a jugal bone, and the whole arch is formed by a backward process of the maxilla which runs back as far as the glenoid cavity and articulates with the squamosal.

The nasals are relatively short. They measure 4·5 mm. in length, and the greatest measurement across the two is at the upper end, where it is 3 mm. In front the transverse measurement is 2 mm.

The lacrimal is very small and cannot be satisfactorily made out in this skull, though it can be detected in the sections of the earlier stage.

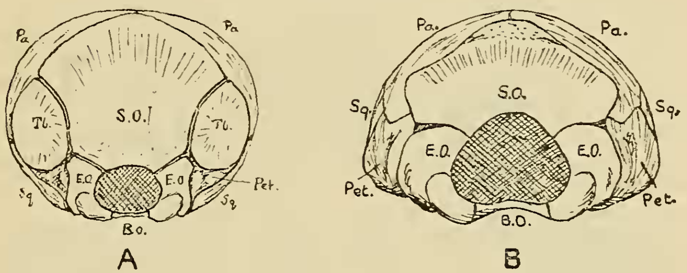
The frontal is relatively small, being only about half the size of the parietal. There is a distinct orbital constriction.

The large parietals each form nearly a quarter of the upper surface of the skull. Each articulates with its neighbour, and with the frontal, squamosal, tabular, and supraoccipital.

The squamosal is of moderate size but very peculiarly shaped. The upper squamous portion is much reduced, and behind the glenoid cavity there is a long posterior descending process which covers the petrosal and extends as far as the exoccipital. In front the squamosal articulates with the maxilla, but forms practically no part of the zygoma.

On the base of the skull the palatines, pterygoids, tympanics, auditory ossicles, vomer, basisphenoid, and basioccipital and exoccipital can be readily made out, but their relations and structure can be better understood from the reconstruction of the earlier stage.

Text-figure 1.



A. Occiput of young *Chrysochloris asiatica*. × 4.
B. Occiput of young *Hemicentetes* sp. × 3·5.

For explanation of lettering see p. 458.

It is necessary, however, to consider more fully the structure of the occiput, as it is unlike that of any other known mammal. When the skull is examined posteriorly there is seen to be a very small basioccipital, a pair of small exoccipitals, and a relatively large supraoccipital, with no distinct interparietal. The relations and shapes of these will be seen in text-fig. 1. On each outer side of the supraoccipital is a rounded bone of moderate size which I regard as the tabular. It is a membrane-bone which articulates with the supraoccipital, the parietal, the exoccipital, and partly covers the petrosal or periotic. At this stage it does not quite reach the squamosal, but not improbably in a slightly more advanced stage it may be found to articulate with the squamosal. Whatever be the nature of this bone, it quite certainly, as will be seen later, is not formed from any part of the ear-capsule, and as it certainly occupies the exact position of the tabular in Therapsid and other early reptiles, it seems well to apply this name to it. As a large tabular occurs in

Cynodonts we may infer that the early mammals still retained it, and possibly *Chrysochloris* and its ancestors have never lost this ancestral character which all other known mammals have lost.

The occiput of *Chrysochloris* is very interesting when compared with its supposed ally *Hemicentetes* (text-fig. 1, B). It will be observed that the most striking difference is the entire absence of even a rudimentary tabular, whose place is occupied by lateral extensions of the supraoccipital and parietal. There are also considerable differences in the relative sizes of the other elements.

Membrane-bones of the base of the skull of the newly-born Chrysochloris hottentota.

The skull of the newly-born *Chrysochloris hottentota* is now represented by 710 transverse sections. From sections 1 to 316 the series is complete and continuous. Here, unfortunately, the block of paraffin has been placed in the microtome in the reversed position and a wedge-shaped section of considerable thickness has been removed. Between sections 372 and 373 about eight sections are missing. Though these imperfections have increased the difficulty of reconstruction, they have fortunately not resulted in the loss of any fact of importance. In the reconstructions I have made, the gaps have been restored, as can be done with complete confidence, and the slight obliquity of the posterior half of the skull corrected.

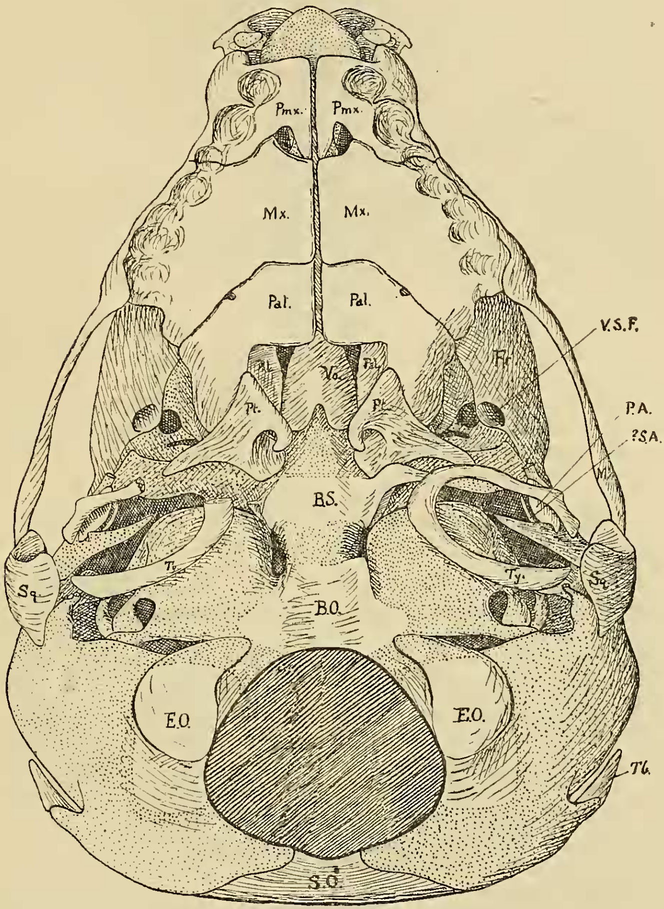
As there is nothing of importance to be seen on the upper side of the skull that is not better seen in the slightly older dissected skull, I shall confine my description to the interesting condition of the base.

The whole palate is relatively shorter and broader than in the older stage. The premaxilla is already well ossified, and has two large open sockets for the 1st and 2nd developing milk-incisors. The cavity for the third developing tooth is only partly formed by the premaxilla, and partly by the maxilla. There seems little doubt, however, that this 3rd tooth is also, as has been generally held, an incisor. The palatine process is rather short, and there is a fairly large anterior palatine foramen.

The maxillary bone has a very broad but rather short palatal plate. There are distinct concavities for part of the 3rd milk-incisor, the milk-canine, the three milk-premolars, and for the 1st true molar. The dental lamina which is going to form the 2nd and 3rd molars is not at this stage supported by bone. From the lamina of bone which forms the outer protection for the dental germs, there is continued backwards the process of bone which forms the zygomatic arch. There is no distinct jugal.

The palatine is seen as a fairly large bone behind the maxillary. The plates forming the secondary palate are well developed, and form the bony borders of the wide choana. Between the deeper portions of the palatines, the relations of which will be better understood from the sections, is seen the

Text-figure 2.



Reconstruction of base of skull of *Chrysochloris hottentota* (newly born) showing the membrane-bones. Portions of the right tympanic and the right basisphenoidal processes have been removed to show the underlying parts. × 12.

For explanation of lettering see p. 458.

vomer. Superficial to the posterior part of the palatine is the peculiarly shaped pterygoid. The main part of the bone is continued backwards from the palatine. A long slender outward process extends underneath the alisphenoid and in close relation to it. Downwards and backwards there passes a strong hooked process which supports the soft palate. The general shape will be readily understood from the restored figure (text-fig. 2).

External to the pterygoid and posterior to it is seen the large bony ring of the tympanic. It forms about $\frac{7}{8}$ of a circle. Lying between it and Meckel's cartilage is seen the prearticular or "goniale" of Gaupp; and immediately internal to the prearticular is a slender splint of bone which has not, so far as I am aware, been previously observed in mammals. It may represent the surangular of the reptilian jaw.

External to the tympanic is seen the developing squamosal. It curves round the auditory region, and in the figure is seen extremely foreshortened. In the slightly older skull the squamosal passes much further downwards and inwards and protects the whole of the posterior tympanic region which at this stage is exposed.

Behind the auditory capsule is seen the developing tabular; it is in close association with the anterior border of the supra-occipital.

In the figure given the only other membrane-bone seen is the frontal, a considerable part of whose lower border is shown. A large foramen shown is occupied by a venous sinus.

Chondrocranium and cartilage-bones of the newly-born Chrysochloris hottentota.

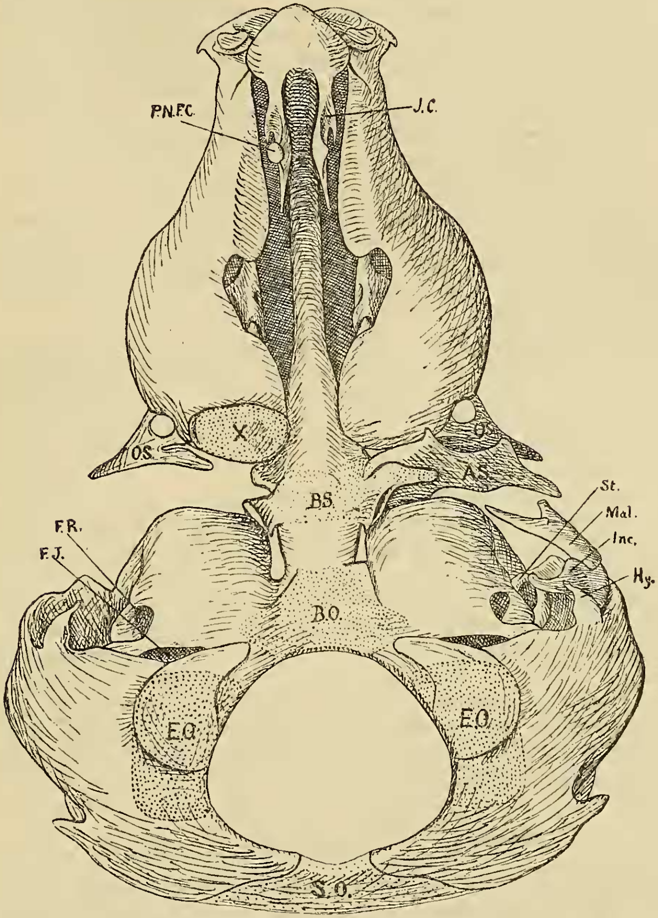
Text-figure 3 shows a reconstruction of the chondrocranium, almost all the membrane-bones having been removed. The most striking general features are the great size of the occipital and auditory regions, the very small size of the orbitosphenoid, and the well-developed condition of the nasal capsules.

The internal structure of the nasal capsule is to some extent revealed in the figures of sections given. In the reconstructed figure the most interesting feature shown is the primitive structure of Jacobson's cartilage. It will be observed that there is, as in marsupials and a few lowly-organised Eutherians, an outer bar which is, however, not quite completely formed. There is a small posterior nasal-floor cartilage.

The orbitosphenoid is unusually small and does not extend far backwards as it does in marsupials and primitive Eutherians. It has a foramen rotundum for the rudimentary optic nerve.

On the base of the posterior part of the nasal capsule is a large membrane-bone of doubtful significance. Text-fig. 3 shows the appearance of the bone as viewed from below after the removal of the vomer, palatine, pterygoid, and alisphenoid. In the figures of sections given (Pls. I., II., figs. 6–8) the relations of the bone to the nasal capsule, to the orbitosphenoid, and to the nasal septum, in addition to the relations to the membrane-bones and the alisphenoid, can be fully understood.

Text-figure 3.



Reconstruction of base of skull of *Chrysochloris hottentota* (newly born) with the membrane-bones removed. On the right side the auditory ossicles have also been removed and part of the basisphenoidal process and the whole of the alisphenoid. The posterior nasal-floor cartilage has also been removed from the left side. × 12.

For explanation of lettering see p. 458.

Being above the alisphenoid, the bone is manifestly not one of the pterygoid group of bones. It is much too far back to be the homologue of the reptilian paired vomer; and it cannot be the septomaxillary. It is no doubt the same bone as Parker found in a number of mammals and referred to as the postero-lateral vomer; but it is no part of the true vomer. Considering how very large a membranous ossification is formed in connection, as we shall see, with the basisphenoid, one may think of the possibility of this being a membranous exostosis in connection with the presphenoid, though at this stage, and even in the later one represented by the small skull dissected, there is no ossification of the cartilaginous presphenoid. In the meantime I think it safest to leave the significance of the bone as very doubtful.

The alisphenoid is fairly well developed but very narrow, and much more like a columella cranii than in any other mammal I know. It is still mainly cartilaginous, though commencing to ossify along the posterior border, and at its inner end there is considerable ossification which cannot altogether be separated from the ossification in membrane which is spreading out from the basisphenoid.

The basisphenoid is chiefly remarkable for the large membranous exostosis which forms a large process extending downwards and outwards. This process may be regarded as a basisphenoidal process comparable to the basisphenoidal process of many reptiles in having a true articulation with the pterygoid.

The auditory ossicles are relatively large.

The general structure of the auditory region will be more readily understood from the sections. The tegmen tympani is feebly developed.

The most interesting feature of the occiput is the fact that only a relatively small part of the supraoccipital is preformed in cartilage. The greater part is a membranous exostosis which fills in the median portion between the two sides. It might be argued that this median part is really the interparietal, but from the condition seen in the later states it seems better to look on the ossification as a supraoccipital in which only the lateral parts have a cartilage basis.

Description of the more important sections.

As I have in my previous paper figured and described the cartilages in connection with Jacobson's organ, and as the posterior part of the nasal capsule has a very complicated arrangement of turbinals which would require for the complete solution of its significance a much fuller comparison with other mammalian types than is at present possible, I shall leave any detailed account of the nasal cartilages till some future time.

Figures 1–6 (Pl. I.) represent sections 131, 185, 238, 280, 302, and 316 respectively, and show the general arrangement of the nasal cartilages.

Fig. 1, which is through the middle part of Jacobson's organ, shows the small posterior nasal-floor cartilage. The anterior part of the maxilla is seen inside the premaxilla.

Fig. 2 shows the small procumbent inferior turbinal. The small developing 1st milk-molar is seen, and the very slender lacrimal duct.

Fig. 3 is through the anterior part of the palatine. The maxilla has the outer portion which protects the developing 3rd milk-molar no longer attached to the main part above.

Fig. 4 is through the plane of the rudimentary eye. The moderately large lacrimal gland is cut across. The relative positions of the palatine, maxilla with its zygomatic process, the vomer, and the frontal are shown.

Fig. 5 is through the anterior part of the pterygoid, and shows the relations of the palatine to the vomer internally and to the pterygoid inferiorly.

Fig. 6 is through the posterior end of the vomer. Above the vomer and the palatine is seen the problematic bone previously mentioned. It is seen to be in close relation to the nasal capsule and almost in contact externally with the spheno-palatine ganglion. A large venous sinus is seen passing out of the frontal bone.

Fig. 7 is a little posterior to the section shown in fig. 6, but not quite in the same plane, as already mentioned. The problematic bone is seen to be of large size, lying above the pterygoid and the posterior end of the palatine.

Fig. 8 (Pl. II.) is through the anterior part of the Gasserian ganglion. The alisphenoid is cut down the middle. The lower end is ossifying by exostosis. Below the alisphenoid is seen the pterygoid. Above these two elements and below the posterior end of the nasal capsule, is the large problematic "lateral vomer." Its upper outer angle is in close relation with the lower inner end of the orbitosphenoid.

Fig. 9 is through the anterior end of the auditory capsule and shows the cochlea in section. The basisphenoid shows part of the lateral exostosis which supports the capsule. The tympanic bone is seen cut across at both the outer and inner ends of the long flattened tympanic cavity. Inside the upper end of the tympanic is seen the curved prearticular or goniale which embraces Meckel's cartilage. Along the inner edge of this prearticular is another slender splint of bone which may represent the reptilian surangular. Above the prearticular is Meckel's cartilage, and inside this latter is seen the small chorda tympani nerve. External to Meckel's cartilage is shown the large cartilage which forms the articular end of the dentary, and above this is seen the posterior end of the zygomatic process of the maxilla and the anterior end of the squamosal. The section is through the main part of the external auditory meatus, which is seen surrounded by a series of cartilages belonging to the external ear.

Fig. 10 is through the posterior part of the malleus. It shows the relations of the squamosal to the parietal and maxilla, and of the hyoid to the VIIth nerve and to the tympanic.

Fig. 11 is through the incus and the stapes. The stapes is seen pierced by the large stapedial artery. The incus is large and is seen mainly covered by the squamosal. The VIIth nerve is seen cut in three places, the inner part being continuous with the geniculate ganglion. In the lower part of the section is seen the large ganglion of the vagus nerve.

Fig. 12 shows the tabular bone and its relations to the supra-occipital, exoccipital, and auditory capsule. Whatever be its significance, it has manifestly, as will be seen, nothing to do with the auditory capsule.

Concluding observations.

The skull of *Chrysochloris* is in part a primitive, and in part a specialised and degenerate type.

It is primitive in the structure of Jacobson's cartilage, in the feeble development of the inferior turbinal, in the simple columella-like alisphenoid, in having a large maxillary zygomatic process, in the possession of a large complicated pterygoid which articulates with a large basisphenoidal process, and in the possession of a distinct tabular bone.

It is degenerate and specialised in the rudimentary condition of the orbitosphenoid, in the loss of the ectopterygoid inter-parietal, and jugal, and the lack of development of a zygomatic process of the squamosal.

The examination of the skull confirms the result of the examination of Jacobson's organ and its relations in showing that *Chrysochloris* is not a near ally of *Centetes*, and that it is not an Insectivore. Further, it is not allied to the Menotyphla, and ought to be placed in a distinct order Chrysochloridea.

Explanation of Lettering of Text-figures and Plates.

Art.D. articular head of dentary; *A.S.* alisphenoid; *Aud.* auditory capsule; *B.O.* basioccipital; *B.S.* basisphenoid; *E.A.* external auditory meatus; *E.O.* exoccipital; *F.J.* foramen jugulare; *F.R.* fenestra rotunda; *Fr.* frontal; *G.G.* Gasserian ganglion; *G.X.* ganglion of Xth nerve; *Hy.* hyoid; *Inc.* incus; *J.C.* Jacobson's cartilage; *l.d.*; *l.g.* lacrimal gland; *Mal.* malleus; *Md.* mandible; *Mk.* Meckel's cartilage; *Mx.* maxilla; *Na.* nasal; *O.* orbit; *O.S.* orbitosphenoid; *P.A.* prearticular; *Pa.* parietal; *Pal.* palatine; *Pet.* petrosal; *Pmx.* premaxilla; *P.N.F.C.* posterior nasal-floor cartilage; *Pt.* pterygoid; *S.A.* surangular; *S.E.* saccus endolymphaticus; *S.O.* supraoccipital; *S.P.G.* spheno-palatine ganglion; *Sq.* squamosal; *St.* stapes; *St.A.* stapedial artery; *Tb.* tabular; *Ty.* tympanic; *V.* Vth nerve; *Vmd.* mandibular branch of Vth nerve; *Vmx.* maxillary branch of Vth nerve; *VII.* VIIth nerve; *Vo.* vomer; *V.S.F.* venous sinus of frontal; ×. problematic bone at back part of nasal capsule.

EXPLANATION OF PLATES I. & II.

Figs. 1–12. Transverse sections of skull of newly-born *Chrysochloris hottentota*.

All sections are 15 times natural size.